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Influence of helping and breeding experience on reproductive performance in the Seychelles warbler: a translocation experiment

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Reproductive success of the cooperative breeding Seychelles warbler (*Acrocephalus sechellensis*) increases with age. This age effect is not due to differential survival or increased reproductive effort, but to accumulated helping and breeding experience. In their first year of breeding, reproductive performance of inexperienced warblers with neither helping nor breeding experience was significantly lower than that of warblers of the same age with either previous helping or breeding experience. Reproductive performance was the same for primiparae with helping experience and for birds with breeding experience. Female primiparae with helping experience or breeding experience built better nests and spent more time incubating than inexperienced females, which led to increased hatching success. Male primiparae with helping experience or males with breeding experience guarded the clutch better than inexperienced males, which led to reduced egg predation. Even-aged warblers with different previous experiences were transferred to unoccupied islands, where birds started breeding immediately in high-quality territories. The experiment showed that birds with helping experience produced their first fledgling as fast as experienced breeders, and significantly faster than inexperienced birds. Breeding performance did not improve further with experience after the first successful breeding attempt. Only birds with previous breeding experience who paired with inexperienced birds, were likely to change mate. The other pair combinations remained stable. Thus, primiparous birds with helping experience have greater lifetime reproductive success than inexperienced primiparae of the same age. This experiment shows that helping behavior has not only been selected for in the context of promoting an individual's indirect fitness, but also in the context of gaining helping experience which translates into improved reproductive success when a helper becomes a breeder. *Key words:* breeding experience, cooperative breeding, experimental removal, helping experience, reproductive success, Seychelles warbler. *[Behav Ecol 7:326–333 (1996)]*

The breeding performance of birds is known to improve with age and experience (Harvey et al., 1988; Newton et al., 1981; Nisbet et al., 1984; Perrins and McCleery, 1985; Pyle et al., 1991; Raveling, 1981; Wooller et al., 1990). Young inexperienced birds in particular tend to breed less successfully than older and more experienced birds. The improvement in breeding success with age is generally attributed to an increase in foraging efficiency and experience (e.g., Coulson and Horobin, 1976; Desrochers, 1992a,b; Lack, 1968; Newton, 1989; Newton et al., 1981; Nol and Smith, 1987; Nur, 1984; Perrins, 1979), but also to an increased reproductive effort (Charlesworth, 1980; Gadgil and Bossert, 1970; Pianka and Parker, 1975; Pugesek, 1981; Williams, 1966), or to the combination of both (Curio, 1983). Learning and/or practicing the skills associated with nest building and caring for eggs and young, may be crucial for future breeding success. Experience could be obtained by previous breeding, or, as in cooperatively breeding species, by helping a breeding pair in rearing a brood (Brown, 1987; Emlen and Wrege, 1989; Koenig and Mumme, 1990). Few studies have investigated the stage at which young breeders fail, whether during incubation (Couls and Thomas, 1985) or during the fledging period or both (Ollason and Dunnet, 1986). One of the major difficulties in trying to assess the factors influencing breeding performance is that effects of age and experience have rarely been separated (Nelson, 1988) and that effects of territory quality and quality of the breeder's partner have not been accounted for. Experimental studies that control for the effects of these variables have yet been performed (Desrochers, 1992a,b; Hunter, 1987; Koenig and Mumme, 1990). The definitive test of the influence of experience on reproduction would involve the translocation of birds of the same age with different types of experiences to places of the same quality where immediate breeding is possible.

The Seychelles warbler (*Acrocephalus sechellensis*) is a rare island endemic, until 1988 known only from Cousin Island (29 ha) in the Seychelles. The island is completely covered with territories. The warbler usually has a one egg clutch and high adult survival. Although warblers can breed successfully in their first year, young birds on their high-quality natal territories are more likely to refrain from breeding. By staying in the natal territory they benefit from higher foraging efficiency leading to increased survival (Komdeur, 1991). Most of these young become helpers, aiding in territory defense, predator mobbing, nest building (mainly females), incubation (females only), nest guarding (mainly males), and feeding of dependent young which are probably not genetically their own offspring (Komdeur, 1994c). Breeding success increases with territory quality (Komdeur, 1992). Experimental removal of helpers has shown that helpers improve reproductive success of their parents and hence gain indirect fitness benefits (Komdeur, 1994c; Komdeur et al., 1995). After controlling for these factors, annual production of fledglings by the same breeding pair increases from 1 to 3 years, remains the same between 3 and 7 years, and decreases beyond 7 years of age (Komdeur, in press). Because the warbler population on Cousin has reached carrying capacity, and given the vulnera-

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bility of one small island in the Indian Ocean, additional populations had been successfully established on the islands of Aride (68 ha) and Cousine (26 ha) in 1988 and in 1990, respectively (Komdeur, 1994a; Komdeur et al., 1991).

In this article I examine the extent to which the increase in reproductive performance with age is due to differences in experience. First, does helping experience translate into improved reproductive success when the helper later becomes a breeder itself? Second, is breeding experience associated with improved reproductive success later in life? I use 14 years of data from an individually marked and genealogically known population. Over a 10 year period, I have been able to record every nesting attempt and its success for all individual warblers, which provides me the opportunity to work on a population of known age and experience. In the analyses, the effects of age, experience of breeding partner, presence of helpers, and territory quality are accounted for. The transfers of even-aged Seychelles warblers with different previous experiences to the unoccupied islands of Aride and Cousine, where birds started breeding immediately in high-quality territories, allowed me to test the extent to which helping, breeding experience, and the quality of the breeding partner contribute to reproductive performance, divorce rate, and future reproductive success. If helping or breeding experience is important, then adults with either previous helping or breeding experience are predicted to perform better on the new islands than inexperienced adults. If so, then experienced pairs are expected to have a lower divorce rate then less experienced pairs. The internal control in this study is the time needed to produce a second fledgling when the transferred birds have become experienced breeders.

METHODS

Study area and data collection

Over the period 23–29 September 1988, 29 color-ringed adult Seychelles warblers (16 males and 13 females) were transferred from Cousin Island to Aride Island by motorboat, a journey of about 45 min. During a 3 day period from 29 June–1 July 1990, 29 color-ringed adult warblers (15 males and 14 females) were transferred from Cousin Island to Cousine Island, a journey of about 15 min. On the islands of Cousin and Aride, the warblers were studied simultaneously from September 1988 to November 1991, and on Cousine from June 1990 to January 1992. On Cousin, the entire population of Seychelles warblers (115–123 groups, 310–400 birds) was under continuous study between January 1981 and July 1994. On Aride, 16–43 groups (29–180 birds) were studied, and on Cousine, 15–17 groups (29–55 birds) were studied. Data presented here were based on individually color-ringed birds. All nestlings were individually color ringed. Fledglings appeared to be nutritionally independent by 3 months of age (Komdeur, 1991). Therefore, I considered them to have reached independence at the end of this period.

Breeding activity

To record breeding activity, all territories on Cousin, Aride, and Cousine were checked every other week for active nests by observing females for 30 min. This observation period was long enough to determine whether birds are breeding; the minimum number of half-minute intervals that a breeding female was involved in either nest building, incubating, or feeding the nestling during this period was two (Komdeur, 1991). Observations on nest building were conducted in the second week after nest initiations. It was also recorded whether a nest was built in a tree fork (comprising two or more branches). Observations on incubation and nest guarding (when the bird was less than 2.5 m from the nest) were conducted in the second week after egg laying. Food provisioning observations started 2 weeks after hatching (nestling period) and were repeated every 3 weeks (fledgling period) until the young died or reached independence. Each observation period comprised three 1 h segments in periods equally spaced over the day: 0630–1030, 1030–1430, and 1430–1830 h. For each 30 s I recorded whether each bird was taking part in each of the above-mentioned categories.

Each territory was checked once per fortnight for the presence of color-ringed birds to determine the proportion of birds that died or survived. Once a bird was missing from its territory, all other territories and vacant areas were checked to assess dispersal. As emigration from the island never occurred, I assumed that missing birds had died. On Aride and Cousine, the island was searched twice a month to plot new territories using a portable tape recorder with a continuous loop cassette of male song to attract birds.

Territory quality

Territory quality, which was not determined by the presence of nest sites and nest predators (Komdeur, 1991, 1994a,c), was measured in terms of insect prey available. Because the warblers are insectivorous, taking 98% of their insect food from leaves (Komdeur, 1991), the quality of a territory depends on insect prey available and amount of foliage. Territory quality (tq) was therefore expressed as mean number of prey invertebrates available within a territory. The method used for measuring territory quality is presented elsewhere (Komdeur, 1991, 1994a). Territories were divided into three categories: low (tq = 0–1500 insects present), medium (tq = 1500–3000), and high quality (tq > 3000).

Definitions of variables

- *Age:* age (years) of the bird, based on known hatching date.
- *Helping status (previous year):* whether a bird had been a helper in a previous year at all stages during reproduction (females: from nest building to feeding young after fledging; males: from guarding the egg to feeding young after fledging) and therefore had helping experience.
- *Breeding status (previous year):* whether a male or female had fledged young of its own in a previous year and therefore had breeding experience.
- *Inexperienced bird:* a bird with neither helping nor breeding experience.
- *Primiparous bird:* a bird breeding for the first time in life.

Removal experiments

The purpose of the present analysis of the removal experiments is to test the extent to which helping and breeding experience, and the quality of the breeding partner, contribute to reproductive performance on the newly colonized islands. Birds between 3 and 5 years of age and with different previous experience were transferred (Table 1). During the first 2 months following translocations, mate switching was common. Thereafter stable pairs were formed, which comprised birds with different types of experience (Table 2). By the end of November 1988, 16 territories had been established on Aride; 13 were occupied by pairs, one by a male with helping experience, and two by single inexperienced males. By the end of August 1990, 15 territories had been established on Cousine; 14 were occupied by pairs and one by a single inexperienced male. During the entire study pe-

Table 1
The number of male and female Seychelles warblers with different types of experiences translocated to Aride in September 1988 and to Cousine in June 1990

	Aride	Cousine	Total
Females			
Inexperienced	3	1	4
Helping experience	3	5	8
Breeding experience	7	8	15
Males			
Inexperienced	3	3	6
Helping experience	3	4	7
Breeding experience	10	8	18
Total	29	29	58

Table 2
Stable pair formations comprising birds with different types of previous experiences on the islands of Aride and Cousine 2 months after translocation, and mean quality of territories held by these birds during the first 15 months following the transfers

Past experience (male × female)	Aride	Cousine	tq ($\times 10^3$)
Breeding × breeding	4	4	433 ± 63
Breeding × helping	3	3	427 ± 44
Breeding × inexperienced	3	1	438 ± 47
Helping × breeding	2	2	419 ± 70
Inexperienced × breeding	1	2	477 ± 69
Helping × helping	—	2	479 ± 27
Helping × —	1	—	390
Inexperienced × —	2	1	460 ± 44
Total	16	15	

riod, all birds stayed alive and all were occupying high-quality territories (Table 2). There was no significant variation in quality of territories held by inexperienced birds, experienced helpers, and experienced breeders. The breeding performance of each pair is exactly known for the first 17 months following the transfers. During this period, no helpers assisted the breeding pair in raising broods, and the ages of breeding birds remained within the 3–7 year age interval, that is, the period during which annual reproductive success remained constant for both males and females (Komdeur, in press). Because I did not need to control for the effects of territory quality, helpers, and age on breeding performance, I treated the data from both islands as one data set. I compared reproductive performance of males and females with different previous experience. These birds were paired with the same breeding partner during the 17 months following pair formation.

Data analyses

To control for age effects when investigating the effects of helping and breeding experience on reproductive success on Cousin Island, I compared 4 year old experienced breeders with primiparous 4 year olds, some of which had been experienced helpers. All investigated birds were occupying low-quality territories, were paired with an experienced breeder, and did not receive assistance from helpers. I was not able to compare 3 year old experienced breeders with inexperienced 3 year olds, because of low sample sizes of experienced 3 year old breeders (females: 0; males: 3).

Tests on nest construction, incubation, nest guarding, and nest loss were based on the first breeding observation for each breeding bird to avoid pseudoreplication and bias toward improved breeding performance due to improved experience with repeated nesting attempts. Unless stated otherwise, means are expressed with standard deviations, probability values are two-tailed, and the null hypothesis was rejected at $p < .05$.

RESULTS

Influence of helping and breeding experience on reproductive performance on Cousin

Table 3 shows the influence of helping and breeding experience on reproductive performance of 4 year old Seychelles warblers on Cousin Island. All birds were occupying low-quality territories and paired with experienced breeders. In both male and female primiparae, the annual nest attempts, and in males, the probability of producing a clutch by his partner, were independent of previous helping experience. Helping experience did enhance breeding success in both sexes. Birds with helping experience produced more nestlings, fledglings, and independent young. Females with helping experience had a higher probability of producing and hatching a clutch than inexperienced females. This was not due to more time spent guarding the clutch by the male, but to better nest construction (Table 3, Figure 1). All nests from females with helping experience were solidly built in forks of trees and were not blown out by gusty winds either before or during incubation. None of the nests built by inexperienced females were built in forks, but between a thin leaf stalk and a tree branch, resulting in higher nest losses. Also, females with helping experience spent more time incubating the clutch than inexperienced females. Females with breeding experience had a higher probability to hatch a clutch when they bred with males with helping experience than when they bred with inexperienced males. All these females built solid nests in tree forks and spent the same time incubating. Males with helping experience spent more time guarding the clutch against predators than males without helping experience, resulting in higher hatching probability.

Seychelles warblers with either helping or breeding experience had similar reproductive success. They produced significantly more independent young than inexperienced birds of the same age (Table 3). Experienced female breeders paired with experienced male breeders showed the same nest attempts as females paired with males with helping experience, and produced fewer clutches than females paired with inexperienced males. Compared with birds with helping experience, experienced breeders had the same probability of producing a clutch, spent the same time incubating and nest guarding, had the same hatching and fledging success, and had the same probability of raising fledglings to independence. Clutches laid by experienced female breeders had significantly higher hatching success than clutches laid by inexperienced females paired with experienced male breeders, because their nests were built in tree forks and not destroyed. Also, clutches laid by experienced female breeders had higher hatching success if these females were paired with males with either helping or breeding experience than if they were paired with inexperienced males. Males with either helping or breeding experience guarded the clutch better than inexperienced males. For both females and males, the mean number of fledglings produced on Cousin Island the following year did not increase with experience (Table 3).

In conclusion, it seems that a bird with breeding experience can improve its reproductive success by pairing with a bird

Table 3
Influence of helping and breeding experience on reproductive performance in 4 year old breeding Seychelles warblers on Cousin Island

	Inexperienced bird (1)	Experienced helper (2)	Experienced breeder (3)	*p* 1 *v.* 2	*p* 1 *u* 3	*p* 2 *u* 3
Females						
Nest attempts	1.33 (0.50)	1.56 (0.24)	1.55 (0.16)	NS	NS	NS
Proportion nests in tree fork[a]	0.0	1.0	1.0	<.001	<.001	NS
Proportion with clutch	0.25	0.93	1.00	<.001	<.001	NS
Clutches	0.33 (0.17)	1.44 (0.18)	1.55 (0.16)	<.001	<.001	NS
Proportion nests blown out[a]	0.67	0.11	0.0	<.05	<.01	NS
Proportion incubating[a]	0.38 (0.05)	0.49 (0.08)	0.49 (0.09)	<.005	<.005	NS
Proportion nest guarding[a]	0.48 (0.13)	0.46 (0.10)	0.51 (0.09)	NS	NS	NS
Hatching success	0.00	0.92	0.94	<.01	<.01	NS
Nestlings	0.00 (0.00)	1.33 (0.17)	1.46 (0.21)	<.001	<.001	NS
Fledging success	—	0.92	0.88	—	—	NS
Fledglings	0.00 (0.00)	1.11 (0.20)	1.27 (0.20)	<.001	<.001	NS
Proportion independent young	—	0.82	0.86	—	—	NS
Independent young	0.00 (0.00)	1.00 (0.17)	1.09 (0.16)	<.001	<.001	NS
Fledglings next year/female	0.56 (0.18)	0.78 (0.14)	0.67 (0.14)	NS	NS	NS
n	9	9	11			
Males						
Nest attempts	1.50 (0.19)	1.33 (0.17)	1.00 (0.00)	NS	.019	NS
Proportion nests in tree fork[a]	1.0	1.0	1.0	NS	NS	NS
Proportion with clutch	1.00	0.83	1.00	NS	NS	NS
Clutches	1.50 (0.19)	1.11 (0.20)	1.00 (0.00)	NS	.019	NS
Proportion nests blown out[a]	0.0	0.11	0.13	NS	NS	NS
Proportion incubating[a]	0.47 (0.08)	0.53 (0.08)	0.51 (0.01)	NS	NS	NS
Proportion nest guarding[a]	0.12 (0.06)	0.55 (0.01)	0.51 (0.08)	<.001	<.001	NS
Hatching success	0.08	1.00	1.00	<.001	<.001	NS
Nestlings	0.13 (0.13)	1.11 (0.20)	1.00 (0.00)	<.001	<.001	NS
Fledging success	1.00	0.90	0.88	NS	NS	NS
Fledglings	0.13 (0.13)	1.00 (0.24)	0.88 (0.13)	<.01	<.001	NS
Proportion independent young	1.00	0.88	0.75	NS	NS	NS
Independent young	0.13 (0.13)	0.89 (0.20)	0.62 (0.18)	.007	<.041	NS
Fledglings next year/male	0.57 (0.19)	0.63 (0.17)	0.69 (0.15)	NS	NS	NS
n	8	9	8			

All birds were occupying low quality territories and paired with an experienced breeder. Statistical significance of comparisons determined by contingency analyses (proportion data) or *t* tests; NS = not significant.

[a] Values based on first attempts.

with either helping or breeding experience, instead of with an inexperienced bird.

Costs and benefits of early or late breeding on Cousin

Although the samples are small, the relative costs of producing fledglings appeared to be the same for birds with helping as for birds with breeding experience. In both males and females, the proportion of 3 year old primiparae with helping experience, which had fledged young in their third year but not in the following year, was the same as that of 3 year old experienced breeders [females: 0.00 (0/4) versus 0.09 (1/11); males: 0.00 (0/3) versus 0.11 (1/9)].

Table 4 illustrates the effect of costs and benefits of early or late breeding in terms of production of fledglings during 5 years on low-quality territories, which is the average adult life expectancy of warblers on these territories (Komdeur, 1992). Reproduction rates from this study were used in the calculations. Two points are worth noting: (1) early breeding is better than delayed breeding; 3 year old inexperienced primiparae produced significantly more fledglings over their estimated lifetime than 4 year old inexperienced primiparae, and (2) helping benefits are greater than nonhelping benefits; 4 year old primiparae with helping experience produced significantly more fledglings over their lifetime than inexperienced 4 year old primiparae, and they produced the same number of fledglings as 3 year-old inexperienced primiparae.

Translocation experiments

Initial pair formations and divorce rates on Aride and Cousine
The birds transferred to Aride and Cousine formed pairs and began to establish territories within days, and in some cases within hours after being released. On both islands, successful nesting started in most territories within a few weeks, and in some territories within 3 days after release. The first young on Aride (twins) and Cousine were hatched by experienced breeders, 4 and 3 weeks after the transfer, respectively. All birds had been resighted within 2 months after the translocations. Birds with different breeding experiences formed pairs and commenced nest building within 2 weeks. Pair formation involved several switches of partners. The decision to change partners depends on previous breeding success with that partner (Figure 2). All pairs that produced their first nestling during the first nesting attempts, and all pairs, apart from one, that produced their first nestling during their second nesting attempt, remained together during the entire study period, or until one of the birds died. However, two out of the eight pairs that failed to produce their first nestling during the second nesting attempt also remained together. All

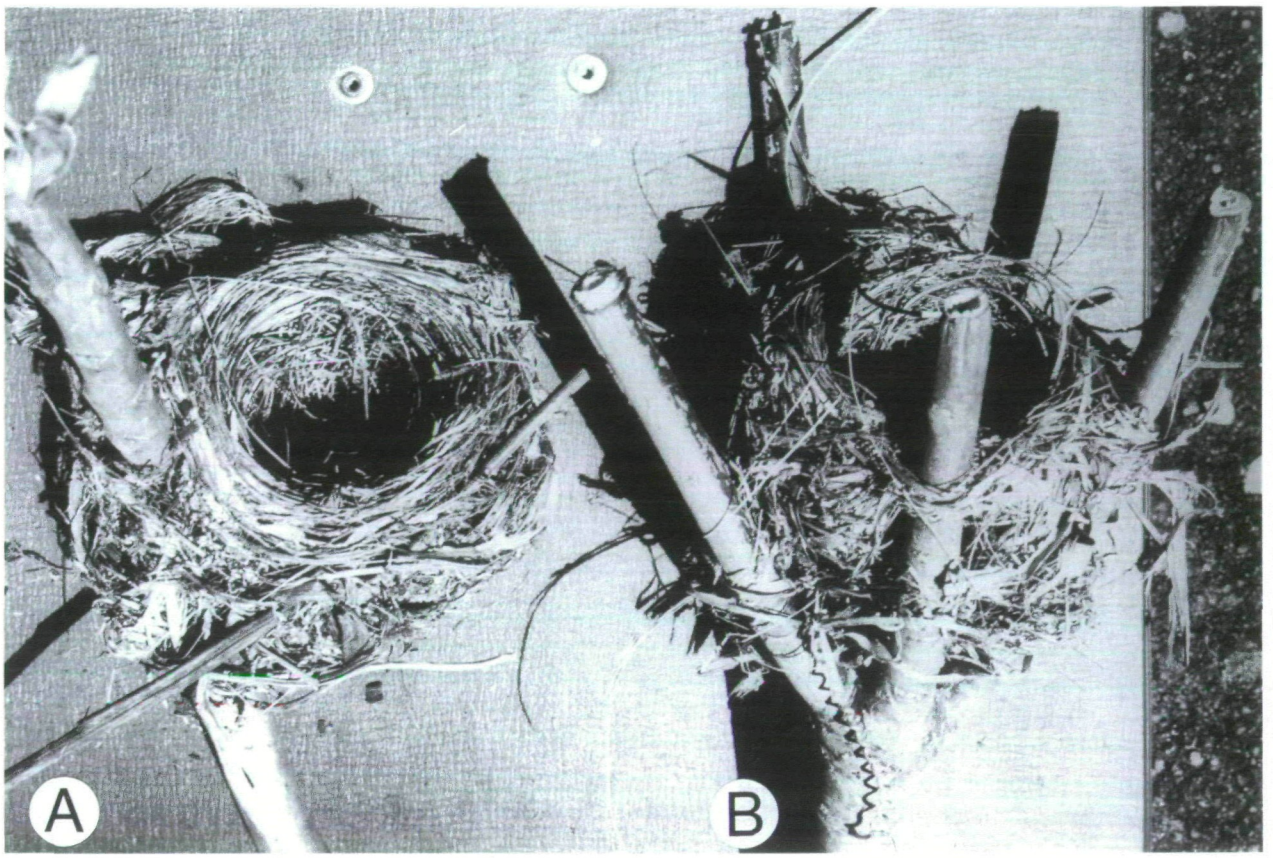

Figure 1
(A) Nest built between a thin leaf stalk and a tree branch that was the first nest built by a 4 year old inexperienced female Seychelles warbler on Cousin Island. (B) Nest built in a tree fork which was the first nest built by a 4 year old female Seychelles warbler with helping experience on Cousin Island.

Table 4
Lifetime production of fledglings (SE) of Seychelles warblers with no helping experience that first bred at age 3 or 4 years, and of warblers with helping experience that first bred at 4 years of age

Age	3-year-old primiparous inexperienced bird (1)	4-year-old primiparous inexperienced bird (2)	4-year-old primiparent with helping experience (3)	*p* 1 *u.* 2	*p* 1 *u.* 3	*p* 2 *u.* 3
Females						
3	0.56 (0.18)	0.00 (0.00)	0.15 (0.06)[a]	<.01	<.01	<.001
4	0.89 (0.11)	0.00 (0.00)	1.11 (0.20)	<.001	NS	<.001
5	1.00 (0.22)	0.56 (0.18)	0.78 (0.14)	NS	NS	NS
Total	2.45 (0.24)	0.56 (0.18)	2.04 (0.10)	<.001	NS	<.001
n	9	9	9			
Males						
3	0.50 (0.22)	0.00 (0.00)	0.15 (0.02)[a]	<.05	NS	<.001
4	0.67 (0.21)	0.14 (0.13)	1.00 (0.24)	NS	NS	<.01
5	1.00 (1.00)	0.57 (0.19)	0.63 (0.17)	NS	NS	NS
Total	2.17 (0.17)	0.71 (0.17)	1.78 (0.35)	<.001	NS	<.05
n	6	7	8			

Annual production (SE) of fledglings are known data, and the birds were paired with experienced breeders. Statistical significance of comparisons determined by *t* tests; NS = not significant.

[a] Indirect fitness gains from helping (Komdeur, 1994c).

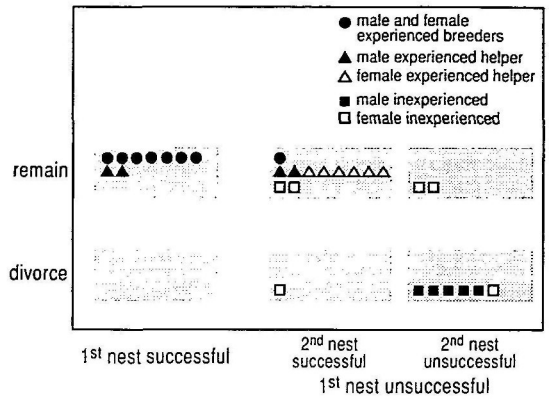

Figure 2
Effect of breeding success on divorce rate of Seychelles warblers with different types of past experiences on the islands of Aride and Cousine. Divorces were measured during the first 2 months following translocations.

pairs that comprised experienced breeders (n = 8) or experienced breeder with an experienced helper (n = 10) remained together. Of the pairs comprising an experienced breeder with an inexperienced bird, only 36.4% (n = 11) remained together. Divorce rates of pairs that failed to produce nestlings during the first and second nesting attempt were high; six of the eight pairs split up. These pairs all comprised an experienced breeder and an inexperienced bird. In six cases the experienced breeder (five times the female, and once the male) left the territory to seek a new partner. In conclusion, all divorces occurred after the second breeding attempt.

Previous experience and reproductive performance

The prediction is that on the islands of Aride and Cousine, inexperienced birds paired with experienced partners will have a lower breeding success than birds with either previous helping or breeding experience paired with experienced partners. The time between pair formation and building the first nest was independent of previous experience of the breeding pair (Figure 3A). All pairs started nest building within 2 to 3 weeks after pair formation. The four inexperienced females built their first nests between a thin leaf stalk and a tree branch, whereas the 21 females with either helping or breeding experience built their nests solidly in tree forks. All first nests from inexperienced females were lost due to heavy rains and gusty winds, whereas the first nests from experienced females remained intact during the incubation and the nestling periods. As a consequence, the time between pair formation and the production of the first fledgling was dependent on previous experience of the breeding pair (Figure 3A). For pairs comprising a male with breeding experience and an inexperienced female it took 3.7 times longer to produce their first fledgling than for pairs consisting of a female with breeding experience and an inexperienced male. The average number of nest building attempts between pair formation and the production of a fledgling was 8.3 (0.8) and 5.7 (1.3), respectively. Overall, pairs comprising an experienced breeder and an inexperienced mate needed a significantly longer time to produce their first fledgling than those comprising an experienced breeder and an experienced helper, or those comprising two experienced breeders (Figure 3A). For pairs comprising an experienced breeder and an experienced helper it took slightly longer to produce their first fledgling than for pairs consisting of two experienced breeders. The time needed to produce the first fledgling was the same for pairs comprising a male with breeding and a female with helping experience as for those comprising a male with helping experience and a female with breeding experience.

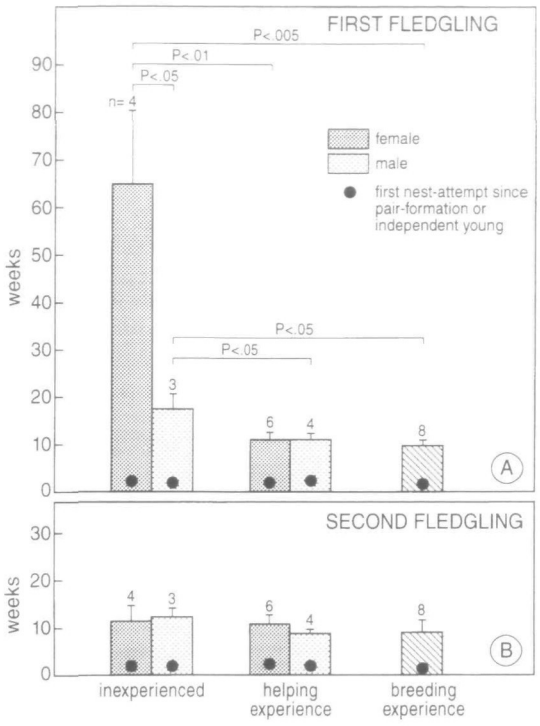

Figure 3
(A) The number of weeks between pair formation and the production of the first nest and first fledgling on the islands of Aride and Cousine plotted for male and female birds with different past experience. (B) The number of weeks between independence of first fledgling and the production of a new nest and second fledgling on the islands of Aride and Cousine plotted for the same male and female birds as in (A), who have become experienced breeders. In both figures, the birds were between 3 and 7 years of age (i.e., the period during which there are no age effects on reproduction), paired with the same experienced breeding partner, and did not receive assistance from helpers. Statistically significant comparisons determined by Mann-Whitney U tests. Only significant differences are plotted.

By definition, all inexperienced birds and birds with previous helping experience became experienced breeders after having produced their first fledgling. After the first successful nest, all nests (n = 25) were built in tree forks and resulted in the production of a fledgling. This was also shown by the observation that the time between reaching independence of the first young and the production of a second fledgling was the same for all pairs (Figure 3B).

DISCUSSION

Reproductive performance in relation to helping and breeding experience

Older Seychelles warblers produced significantly more fledglings as compared to younger birds (Komdeur, 1991, in press). The enhanced reproductive success in the later years is not due to differential survival and increased reproductive effort (Komdeur, in press), but to accumulated helping and breeding experience, and to a higher probability that an older, nonbreeding bird will become a helper (Komdeur, 1991, 1996). Because inexperienced birds occupy the same quality territories and are as efficient in foraging as birds with helping or

breeding experience of the same age (Komdeur, 1991), the reason for the observed differences in reproductive success has to be sought in differences in the bird's ability to breed successfully. In this study, environmental effects were minimized, as comparisons were made between reproductive success of breeding pairs occupying the same quality territories. On Cousin Island, inexperienced warblers do less well in their first year of breeding than warblers with either helping or breeding experience. Female primiparae with helping experience built better nests, had a higher probability of laying a clutch, and spent more time incubating than inexperienced females. Better nests prevent the egg from being destroyed by heavy rains and gusty winds. Increased incubation prevents the egg from chilling and retardation and possibly death of the embryo (Nelson, 1966), resulting in a higher hatching success in the Seychelles warbler (Komdeur, 1994c). Male primiparae with helping experience guarded the clutch better, leading to reduced egg predation by Seychelles fodies (*Foudia sechellarum*, weaver birds endemic to the Seychelles), and by two endemic skink species (*Mabuya wrightti* and *M. sechellensis*) (Komdeur, 1994a,c). This resulted in a higher hatching success (Komdeur, 1994c). However, the reproductive performance was the same for primiparae with helping experience as for birds with breeding experience. It seems that reproductive success is determined by the bird's experience with either helping or breeding. The effect of helping or breeding experience on breeding performance was experimentally tested by translocations of birds with different types of experience to suitable unoccupied islands. Birds with helping experience that were paired with an experienced partner produced their first fledgling as fast as experienced breeders, and significantly faster than inexperienced birds paired with an experienced partner.

It could be argued that inexperienced birds are inexperienced because they are of poor quality relative to their contemporaries, which may mean that it is not their inexperience per se affecting their poor reproductive success. The internal control of the translocation experiments controls for this possibility. After the first year of breeding, the annual number of fledglings produced on Cousin Island did not increase with experience, indicating that the birds had acquired breeding experience. Once inexperienced birds had fledged young to independence on the islands of Aride and Cousine, and thus had acquired breeding experience, they subsequently improved their breeding success by producing a second fledgling in the same time interval as birds with either helping or breeding experiences.

In other studies of breeding experience where age was controlled for, some reported positive associations with clutch size and/or fledging success (Ainley et al., 1983; Forslund and Larsson, 1992; Harvey et al., 1985), while others failed to find any effects (Boekelheide and Ainley, 1989; Davis, 1976; Newton et al., 1981; Nol and Smith, 1987). However, these associations may be due to differences between individuals such that superior birds started to breed at an early age, thereby acquiring more breeding experience at a given age as compared to inferior individuals which may start to breed at an older age (Harvey et al., 1985). In the Seychelles warbler, this is not the case. In this study, all birds with breeding experience had only successfully fledged one young in the previous year and not in the years before.

Pair formation and divorce as a function of previous experience

If experience is important for breeding success, an inexperienced individual could do better by pairing with an experienced mate than with one as inexperienced as itself (e.g., Loman, 1984; Petrie and Hunter, 1993). Pair formations after translocations of warblers to previously unoccupied islands suggested that a warbler cannot assess the quality of its partner before breeding. Initially, warblers paired randomly, regardless of previous helping or breeding experience. However, experienced birds paired with inexperienced partners were more likely to divorce than experienced birds paired with partners that had either helping or breeding experience. It seems that the warbler's decision whether or not to divorce depends on previous reproductive success with its mate. If no fledglings were produced during the first and second breeding attempt, the birds readily changed partners. It is the experienced bird deserting its territory and partner, looking for a new partner. Apart from one exception, pairs producing their first fledgling during the first or second breeding attempt did not divorce.

On Cousin Island, however, most pairs (99.1%; $n = 224$; Komdeur, 1991) and all pairs in this study remained together until the death of one of the partners, regardless of previous experience. The reason for an experienced bird not to divorce an inexperienced bird is lack of breeding vacancies (Komdeur, 1992). In addition, by leaving its breeding territory, another bird will take the vacancy within hours, due to the high number of additional nonbreeding adults present (Komdeur, 1992).

Costs and benefits of helping and breeding

According to life-history theory, individuals should begin to reproduce at an age when the net benefits are greater than the net benefits of delaying reproduction (Promislow and Harvey, 1990; Stearns, 1992). Early reproduction can be beneficial if it reduces the probability of an individual dying before any offspring have been produced, or if it increases the number of offspring produced in an individual's lifetime. Early reproduction may be costly if survival, fecundity, or offspring survival are reduced (Harvey and Zammuto, 1985; Stearns, 1992). In the Seychelles warbler, reproductive effort was apparently as costly for inexperienced birds as for birds with helping and breeding experience. The proportion of birds fledging young in the next year was the same for all categories. Because the reproductive payoff is independent of age and previous experience, early breeding on a given quality territory is better than delayed breeding. Birds breeding at an early age produce significantly more fledglings over their lifetime than birds starting to breed at a late age. However, the fraction of older birds that had never fledged young of their own was quite large (Komdeur, in press). Most of these birds had not been able to fill breeding vacancies because of a shortage of breeding territories (Komdeur, 1992; Komdeur et al., 1995). Most birds delaying breeding become helpers instead. The fitness costs of helping are probably small, as survival rates of helpers and nonhelpers of the same age were the same (Komdeur, 1994c). One reason to become a helper is to gain indirect benefits through increased production of the helper's nondescendent kin (Brown, 1980; Emlen and Wrege, 1988; Komdeur, 1994b,c). This study showed that another reason for helping is to gain helping experience, which translates into improved reproductive success when a helper becomes a breeder. Consequently, birds with helping experience have greater lifetime reproductive success than birds without helping experience.

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REFERENCES

Ainley DG, LeResch RE, Sladen WJ, 1983. Breeding biology of the Adelie penguin. Berkeley: University of California Press.

Boekelheide RJ, Ainley DG, 1989. Age, resource availability, and breeding effort in Brandt's cormorant. Auk 106:389–401.

Brown JL, 1980. Fitness in complex avian social systems. In: Evolution of social behavior (Markl H, ed). Weinheim, Germany: Verlag-Chemie; 115–128.

Brown JL, 1987. Helping and communal breeding in birds: ecology and evolution. Princeton, New Jersey: Princeton University Press.

Charlesworth B, 1980. Evolution in age-structured populations. Cambridge: Cambridge University Press.

Coulson JC, Horobin J, 1976. The influence of age on the breeding biology and survival of the arctic tern, *Sterna paradisaea*. J Zool Lond 178:247–260.

Coulson, JC, Thomas C, 1985. Differences in the breeding performance of individual Kittiwake gulls *Rissa tridactyla* (L.). In: Behavioural ecology: ecological consequences of adaptive behaviour (Sibly RM, Smith RH, eds). Oxford: Blackwell; 489–503.

Curio E, 1983. Why do young birds reproduce less well? Ibis 125:400–404.

Davis JWF, 1976. Breeding success and experience in the Arctic skua, *Stercorarius parasiticus* (L.). J Anim Ecol 45:531–535.

Desrochers A, 1992a. Age and foraging success in European blackbirds: variation between and within individuals. Anim Behav 43: 885–894.

Desrochers A, 1992b. Age-related differences in reproduction by European blackbirds: restraint or constraint? Ecology 73:1128–1131.

Emlen ST, Wrege PH, 1988. The role of kinship in helping decisions among white-fronted bee-eaters. Behav Ecol Sociobiol 23:305–315.

Emlen ST, Wrege PH, 1989. A test of alternate hypotheses for helping behavior in white-fronted bee-eaters of Kenya. Behav Ecol Sociobiol 25:303–319.

Forslund P, Larsson K, 1992. Age-related reproductive success in the barnacle goose. J Anim Ecol 61:195–204.

Gadgil M, Bossert W, 1970. Life historical consequences of natural selection. Am Nat 104:1–24.

Harvey PH, Stenning MJ, Campbell B, 1985. Individual variation in seasonal breeding success of pied flycatchers (*Ficedula hypoleuca*). J Anim Ecol 54:391–398.

Harvey PH, Stenning MJ, Campbell B, 1988. Factors influencing reproductive success in the pied flycatcher. In: Reproductive success: studies in individual variation in contrasting breeding systems (Clutton-Brock TH, ed). Chicago: Chicago University Press; 189–200.

Harvey PH, Zammuto RM 1985. Patterns of mortality and age at first reproduction in natural populations of mammals. Nature 315:319–320.

Hunter, 1987. Cooperative breeding in purple gallinules: the role of helpers in feeding chicks. Behav Ecol Sociobiol 20:171–177.

Koenig WD, Mumme RL, 1990. Levels of analysis and the functional significance of helping behavior. In: Interpretation and explanation in the study of animal behavior, vol. 2, Explanation, evolution and adaptation (Bekoff M, Jamieson D, eds). Boulder, Colorado: Westview Press; 268–303.

Komdeur J, 1991. Cooperative breeding in the Seychelles warbler (PhD dissertation). Cambridge: Cambridge University.

Komdeur J, 1992. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. Nature 358:493–495.

Komdeur J, 1994a. Conserving the Seychelles warbler *Acrocephalus sechellensis* by translocation from Cousin Island to the islands of Aride and Cousine. Biol Conserv 67:143–152.

Komdeur J, 1994b. The effect of kinship on helping in the cooperative breeding Seychelles warbler (*Acrocephalus sechellensis*). Proc R Soc Lond B 256:47–52.

Komdeur J, 1994c. Experimental evidence for helping and hindering by previous offspring in the cooperative breeding Seychelles warbler (*Acrocephalus sechellensis*). Behav Ecol Sociobiol 34:31–42.

Komdeur J, 1996. Facultative sex ratio bias in the offspring of Seychelles warblers. Proc R Soc Lond B 263:661–666.

Komdeur J, in press. Influence of age on reproductive performance in the Seychelles warbler. Behav Ecol.

Komdeur J, Bullock ID, Rands MRW, 1991. Conserving the Seychelles warbler by translocation: a transfer from Cousin Island to Aride Island. Bird Conserv Int 1:179–188.

Komdeur J, Castle G, Huffstad A, Mileto R, Prast W, Wattel J, 1995. Transfer experiments of Seychelles warblers to new islands: changes in dispersal and helping behaviour. Anim Behav 49:695–708.

Lack D, 1968. Ecological adaptations for breeding in birds. London: Methuen.

Loman J, 1984. Breeding success in relation to parent size and experience in a population of the hooded crow. Ornis Scand 15:183–187.

Nelson JB, 1966. The breeding biology of the gannet *Sula bassana* on the Bass Rock, Scotland. Ibis 108:584–629.

Nelson JB, 1988. Age and breeding in seabirds. In: Proceedings of the XIXth Ornithological Congress (Ouellet H, ed). Ottawa, Canada: Ottawa University Press; 1081–1097.

Newton I, 1989. Lifetime reproduction in birds. London: Academic Press.

Newton I, Marquiss M, Moss D, 1981. Age and breeding in sparrowhawks. J Anim Ecol 50:839–853.

Nisbet ICT, Winchell JM, Heise AE, 1984. Influence of age on the breeding biology of common terns. Colonial Waterbirds 7:117–126.

Nol E, Smith JNM, 1987. Effects of age and breeding experience on seasonal reproductive success in the song sparrow. J Anim Ecol 56: 301–313.

Nur N, 1984. Increased reproductive success with age in the California gull; due to increased effort or improvement of skill? Oikos 43:407–408.

Ollason JC, Dunnet GM, 1986. Relative effects of parental performance and egg quality on breeding success of fulmars *Fulmarus glacialis*. Ibis 128:290–296.

Perrins CM, 1979. British tits. London: Collins.

Perrins CM, McCleery RH, 1985. The effect of age and pair bond on the breeding success of great tits *Parus major*. Ibis 127:306–315.

Petrie M, Hunter FM, 1993. Intraspecific variation in courtship and copulation frequency: an effect of mismatch in partner attractiveness? Behaviour 127:265–277.

Pianka ER, Parker WS, 1975. Age-specific reproductive tactics. Am Nat 109:453–464.

Promislow DEL, Harvey PH, 1990. Living fast and dying young: a comparative analysis of life-history variation among mammals. J Zool Lond 220:417–437.

Pugesek BH, 1981. Increased reproductive effort with age in the California gull (*Larus californicus*). Science 212:822–823.

Pyle P, Spaer LB, Sydeman WJ, Ainley DG, 1991. The effects of experience and age on the breeding performance of western gulls. Auk 108:25–33.

Raveling DG, 1981. Survival, experience, and age in relation to breeding success of Canada geese. J Wildl Manage 45:817–829.

Stearns SC, 1992. The evolution of life histories. Oxford: Oxford University Press.

Williams GC, 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. Am Nat 100:687–690.

Wooller RD, Bradley JS, Skira IJ, Serventy DL, 1990. Reproductive success of short-tailed shearwaters *Puffinus tenuirostris* in relation to their age and breeding experience. J Anim Ecol 59:161–170.